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THE LIFE HISTORY AND ECOLOGY OF *EUPHYDRYAS GILLETTII* BARNES (NYMPHALIDAE)

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ABSTRACT. Based on studies of several populations, the life stages of the montane butterfly *Euphydryas gillettii* and its natural history and ecology are described. *E. gillettii* shows unusual developmental flexibility in that it can diapause as second, third, or fourth instars, depending on climatic conditions; in addition, one population in a colder habitat is mostly biennial, while others are annual. In spite of this flexibility, the species has limited distribution in isolated populations over a narrow geographical range.

Euphydryas gillettii Barnes occurs in the middle Rocky Mountains, ranging from western Wyoming, through northern Idaho and western Montana, and into Alberta (Ferris and Brown, 1981). While much work has been published on other species of *Euphydryas* in the past 20 years (Ehrlich et al., 1975; Cullenward et al., 1979; Brown and Ehrlich, 1980; Stamp, 1982), little has been known about *E. gillettii*. Until very recently (Williams, 1981; Holdren and Ehrlich, 1981), the only report in the literature on the biology of this species was that of Comstock (1940), which describes the eggs and early instars.

We have studied *E. gillettii* in several locations recently and here report on its life history and ecology. Four populations have been observed extensively: natural populations in the Teton and Beartooth Mountains of Wyoming, and two populations introduced into Colorado from the Teton colony. In addition, several other populations have been visited.

TABLE 1. Width of the head capsule, spine length, and body size for the different instars of *Euphydryas gillettii*.

Instar	Width of head capsule (mm)	Length of spines		Body length moving (mm)
		Shaft (mm)	Setae (mm)	
First	0.44 ± 0.01 (30)	0.02	0.2-0.3	3-4
Second	0.61 ± 0.03 (81)	0.30 ± 0.04 (28)	0.2-0.4	4-6
Third	0.90 ± 0.04 (46)	0.46 ± 0.06 (43)	0.3-0.5	5-9
Fourth	1.17 ± 0.13 (84)	0.69 ± 0.10 (39)	0.5-0.7	9-13
Fifth	1.47 ± 0.18 (39)	0.74 ± 0.10 (42)	0.6-0.9	12-18
Sixth	2.40 ± 0.12 (5)	0.74 ± 0.16 (27)	0.7-1.2	15-30

Study Sites

The Beartooth population lives along a small stream in a montane meadow of 2620 m (8600 ft) elevation. The butterflies fly in an elongate area, roughly 60 m by 240 m, which is surrounded by coniferous forest of primarily *Picea engelmannii*. The highest density occurs in an area of secondary growth, where trees are scattered sparsely through a moist bottom area near the stream.

The Teton population is the largest known for this species. The butterflies are widely scattered over an eastern facing slope at 2100 m (6900 ft) elevation, occurring in an area roughly 400 m by 1500 m of mostly herbaceous vegetation. Streams run down through this slope, and trees, mostly *Picea* and *Populus tremuloides*, grow along the stream beds. Adults are found throughout the slope.

The two Colorado sites are in Gunnison County. One, adjacent to the Rocky Mountain Biological Laboratory at Gothic (2900 m, 9500 ft), is similar to the Teton site. It consists of a moist meadow containing thick stands of willows on an east-facing slope, bounded by spruce forests, the East River, and the cliffs of Gothic Mountain. The second, Pioneer Resort (2700 m, 8800 ft), is less open than either the Gothic or Teton sites, but the flora is similar.

Description of Life Stages

Measurements of the head, spines, and body for the different instars are given in Table 1.

Egg. Nearly spherical; rounded base with sides sloping in to flattened top. Approximately 22 longitudinal ridges which extend most of distance down from apex, with irregular pitting on base; horizontal striations between ridges (Comstock, 1940). Color yellow-green when first oviposited (see Egg Development for color changes). Diameter 0.78 ± 0.02 mm ($n = 11$) and height 0.86 ± 0.04 mm ($n = 11$) (eggmass shown in Fig. 1a).

First Instar Larva. Head blackish brown with few thin, colorless setae. Body pale greenish yellow with colorless setae arising from 12 longitudinal rows of brown papillae. Appearance is of a pale body spotted with brown. Spiracles brown. Anal prolegs darker than other prolegs, which are concolorous with body; true legs brown (Fig. 1b).



FIG. 1. Life stages of *Euphydryas gillettii*: a, egg mass; b, first and second instars (prediapause); c, third instars (postdiapause); d, fourth instars (postdiapause); e, sixth instar prepupa; f, pupa.

Second Instar Larva. Head blackish brown with black setae. Body developing characteristic banding pattern of later instars: dorsal band pale yellow; dorsolateral band brown and irregular; lateral (stigmatal) band dull white; ventrolateral band light brown; and ventral band cream colored. Spiracles blackish brown. True legs brown. Crochets black; anal prolegs brown on outside. Branching spines develop from papillae and simple seta of first instar; shafts of spines light brown with black setae. Rows of spines as follows: one mid-dorsal in dorsal band; two in dorsolateral band, more dorsal row positioned caudal to second, and second on edge of next band; one row in lateral band; and two rows of small spines or tubercles adjacent to each other in ventrolateral band. Spines developed on all thoracic and abdominal segments, with exception of first and third rows, which are missing from thoracic segments (Fig. 1b).

Third Instar Larva. Head capsule black with black setae. Body has same banding pattern of previous instar, but with deeper colors. Ventral band with thin mid-ventral brown line. Prolegs yellow with black crochets; anal prolegs dark brown on outside. Spiracles black. Shafts of spines blackish brown on all rows except mid-dorsal row, in which shafts are yellow-brown (Fig. 1c).

Fourth Instar Larva. Banding pattern further developed with greater contrast: dorsal band lemon yellow; dorsolateral band blackish brown with brown bases to spines; lateral band white with black spiracles; ventrolateral band brown; ventral band pale yellow with brown mid-ventral stripe. True legs black; prolegs yellow with brown bases and black crochets, and anal prolegs mostly black on outside. Shafts of all spines black, though with ring of lighter color at base of each, with yellow on light colored bands and brown on darker ones (Fig. 1d).

Fifth Instar Larva. Colors and patterns as in previous instar, with following exceptions: dorsal stripe bright lemon yellow, dorsolateral band black, spines and setae jet black, and all prolegs yellow but dark on outside.

Sixth Instar Larva. Continued development of previous banding pattern, with sharper contrast between bands. Midventral line blackish brown.

Prepupa. Slight discoloration of last instar, with some shortening and thickening (Fig. 1e).

Pupa. Ground color cream with black markings. Orange markings also occur except on wing cases; they are concentrated on abdominal segments, where there are seven orange warts per segment. Pupae average 16 mm long (Fig. 1f).

Adult. Head and thorax black; abdomen black above and somewhat lighter underneath. Palpi and legs concolorous with distinctive brownish orange color of postmedian band (this color is closest to the reddish orange of color 7B7 in Kornerup and Wanscher, 1978; it is nearly identical to the orange-rufous, color II-11i, of Ridgway, 1912). Antennae black with thin white rings and with yellowish clubs. Dominant color of dorsal wing surface black; veins black; marginal band of orange and submarginal band of white much reduced, often disappearing in secondaries; postmedian band crossing both wings, 3-4 mm wide, and prominent; median spot band white and reduced, disappearing by anal margin; discal cell of primaries with four alternating spots of white and characteristic orange-rufous color, with another spot of each color in postcellular space; secondaries with three spots of each color in cell and postcellular space; basal area black. Underwings with same patterning as above, but black color reduced and spots expanded; this is especially true on secondaries in median to basal area, where there is great expansion of orange-rufous color and where black is limited to borders of spots. Males smaller than females, with forewing length 16.5 to 23 mm (mean = 20.9, $n = 162$); for females, forewing length 20.0 to 25.5 mm (mean = 23.7, $n = 199$) (Fig. 2b).

Ecology

Oviposition. As reported by Comstock (1940), the larval host is *Lo-nicera involucrata* (Rich.) Banks (Caprifoliaceae), a shrub 0.5 to 3 m tall that grows in moist soil in thickets and wooded areas throughout the geographical range of *E. gillettii* and far beyond (e.g., California,

Mexico, Alaska, and Quebec). The leaves are glabrous, short-petiolate, elliptic-oblong to elliptic-obovate in shape, and 5–14 cm long and 2–8 cm wide (Hitchcock et al., 1959). Thus, the leaves are large enough to allow females to move completely to the underside of the leaves when ovipositing. Some authors (e.g., Tietz, 1972) have listed other larval foodplants, but eggs on or oviposition behavior near any plant other than *L. involucrata* is extremely rare. Of more than 600 egg masses seen in the Beartooth population, only four have been found on a plant other than *L. involucrata*; these occurred in 1982 on an unusually large and conspicuous specimen of *Valeriana occidentalis* Heller (Valerianaceae, a family related to the Caprifoliaceae). Post-diapause larvae may wander to other species of plants, however.

Female *E. gillettii* oviposit mostly in late morning. Prior to oviposition they fly slowly above the shrub and herbaceous layer, fluttering near or touching branches that are among the most apparent (highest or densest). They do not appear to follow vegetational edges. While searching for oviposition sites, they occasionally touch plants other than *Lonicera*, but then they usually fly on within 2 sec.

Once a female does find *L. involucrata*, she flutters near the shrub, lands on a leaf, walks on it for a few seconds, and then flutters in the air, landing on the same or a different leaf. This process continues for 1 to 30 minutes, and even when she is blown or chased from the shrub, she returns to the same leaf or to one quite near it. She gradually increases the time spent on one leaf, walking up and down the dorsal surface near the leaf midrib, repeatedly opening and closing her wings, and occasionally moving entirely to the underside of the leaf. After the female backs over or flips sideways to the underside of the leaf, there is an initial quiescent period of a minute or two which generally precedes oviposition. Sometimes she may return to the upper surface after remaining quiescent for a brief time, walk around the leaf again, and perhaps even move to another leaf. When she finally begins ovipositing, she remains motionless with the wings usually held open (Fig. 2b). Oviposition behavior of *E. gillettii* is quite similar to that described for *E. phaeton* (Stamp, 1982). Females appear to spend much time and effort assessing the potential oviposition site; individual females have been observed to spend more than two hours in the above behaviors before actually beginning to oviposit.

The leaves chosen for oviposition are always large and near the top of a growing stem. In the Beartooth population, 51% of the egg masses were on the highest leaf pair and 36% on the next highest leaf pair (2 years, n = 453). Only one of 456 egg masses was found on the upper surface of a leaf, and only 7 of the 62 eggs from that egg mass hatched, while 30 were dislodged. The chosen leaves may or may not have other



FIG. 2. *Euphydryas gillettii*: a, prediapause feeding web, which becomes the hibernaculum; b, ovipositing female; c, parasitized fifth instar prior to emergence of the parasitoid.

egg clusters already on them; in the Beartooth population, 44% ($n = 456$) of all egg masses were on leaves that had another egg mass on the same leaf (23% of all leaves with eggs, $n = 332$), resulting in a mean of 1.37 clusters per leaf. Egg masses are also clumped in *E. phaeton* (Stamp, 1982).

Approximately one-half of all egg clusters touch the leaf midrib. An ovipositing female faces the edge of the leaf and, while moving her abdomen back and forth, touches the lower leaf surface with the tip of the abdomen. If she then touches the midrib or another protruding leaf vein, she may use it as a guide in oviposition. Often she will use a previous egg mass as a guide. She lays the eggs row by row in both directions, and sometimes a second layer or more is oviposited upon the first. The far edge of the egg mass averages 2.0 cm from the edge of the leaf and the near edge 1.1 cm ($n = 52$), a distance which reflects the length of the body (roughly 1.6 cm).

In the Beartooth population, egg clusters have ranged in size from 23 to 310 eggs ($n = 72$), with a mean of 146 (Fig. 1a). In the Teton

population, the average size over a three year period was 130 eggs per mass ($n = 189$), while in Colorado the average was 128 eggs per mass. In contrast, the egg masses of *E. editha* contain 45 eggs on average (Labine, 1968), while those of *E. phaeton* contain 274 (Stamp, 1982). Oviposition in *E. gillettii* proceeds at an average of 3.8 eggs per minute ($n = 48$ clusters), requiring 38 min to lay an average sized cluster; *E. editha* oviposits at a slower rate, needing 30 min to produce its smaller cluster (Labine, 1968). Based on observations of 150 marked female *E. gillettii* seen to display pre-oviposition behaviors or to oviposit at least once, none oviposited more frequently than every other day.

Egg Development. During the course of development in the Bear-tooth population, a mean of 13% of the eggs ($n = 48$ clusters) are lost from the egg mass due to dislodgement or detachment (19 eggs from a 146 egg average). Sometimes the edge of an egg mass peels away from a leaf, but most egg loss occurs where the eggs are more than one layer deep. The variance in egg loss per cluster is high, however, and most clusters lose few eggs. Presumably those eggs which detach from the leaves and fall to the moist, shady, predator-infested soil surface below do not hatch.

In Colorado, up to 30% of the egg masses are lost entirely during the developmental period due to heavy predation. Furthermore, few egg masses escape without some predation; losses of roughly 10 to 20% of the eggs in a mass are common. The predators are the same for the eggs as they are for the larvae: erythroid mites, myrid bugs, beetle larvae, and browsing mammals, the latter including moose and cattle.

The eggs change color during development from a pale straw-yellow when first oviposited, sometimes with a greenish tint, to a distinct gold, and then to darkening shades of red-brown. They become blue-gray about two days before hatching, a color which results from the formation of a dark head capsule beneath the white translucent egg shell.

The eggs hatch from July into September, while the snow begins falling in late August in these mountainous areas. Eggs hatch in 23 to 45 days in the Beartooth population, depending on the exposure of the oviposition site. In Colorado, the majority of the eggs hatch in 18–30 days, although those masses that are produced late in the season develop more slowly. Eggs at the center of the egg mass are the first to hatch, and most eggs hatch within a two day time span (Williams, 1981). A substantial fraction of the eggs, roughly 20% in the Beartooth population, hatch in early September after the leaves of *L. involucrata* have begun to wilt and turn yellow.

Prediapause Larvae. Newly emerged larvae feed partially on the egg shells, and within 24 hours they migrate to the upper surface of the leaf, where they begin forming a communal feeding web (Fig. 1b).

The oviposition leaf is the first feeding site and is the base of the web; it curls inwards and is bound ever more tightly as time passes. Prediapause larvae feed only on the epidermis and parenchyma of the leaves, leaving behind the patterned network of veins. Feeding occurs during the day; nocturnal feeding has not been observed. Gradually more leaves are added to the feeding web by binding lower leaf pairs to the first leaf. In this way the communal web grows larger, sometimes with the incidental binding of grasses and other leaves that are adjacent to the hostplant leaves. The "knots" (Scudder, 1889) thus formed are quite apparent in the field since they generally occur at the apices of the most conspicuous stems (Fig. 2a). Because different egg masses are often oviposited on the same or adjacent leaves, the larvae in a single feeding web may be the products of several different egg masses, even when these egg masses hatch on different dates.

Mortality is high during the prediapause period. Parasitic wasps identified as *Benjaminia* sp. (N. Stamp, pers. comm.) have been collected from the feeding webs, and the above-mentioned predators take a heavy toll. At least 80% of the larvae in the Beartooth population disappear before reaching winter diapause, while 50–60% of the Colorado larvae die or disappear.

Most, if not all, of the larvae that result from a single egg mass remain in the same feeding web overwinter. Though these hibernacula are well attached to the woody stems of the shrubs, most are dislodged by winter snow.

Unlike the larvae of other well-studied *Euphydryas*, which diapause in the fourth instar, *E. gillettii* are apparently able to overwinter in response to environmental conditions as second, third, or fourth instars. For instance, the Beartooth colony, constrained by the rapid onset of winter at the end of the flight period, diapauses (first winter) in the second instar. In Colorado, where the two sites differ markedly in the length of both the larval and the food-plant growing season, the populations diapause at different instars even though they originated from the same parent colony in the Tetons. Like the original population, the larvae at 2440 m in Colorado reach the fourth instar, while at 2920 m they appear to overwinter successfully after the first molt but develop to the fourth instar given a sufficiently long summer (Holdren and Ehrlich, 1981). Overwintering larvae may pass through an extra molt before emergence, as occurs in *E. editha* (M. Singer, pers. comm.).

Postdiapause Larvae. In Colorado and Wyoming the larvae terminate diapause soon after the snow melts, which in most years is late May at 2440 m (8000 ft) and mid-June at 2920 m (9600 ft). The larvae feed on newly formed buds of *L. involucrata*, boring holes into the larger apical buds and consuming entirely the smaller axillary buds

(Fig. 1c). By the time the larvae have molted into the fifth instar in the annual populations, the leaves are slightly expanded, measuring roughly 2 cm in length. In postdiapause fourth instars in the biennial population, the larvae may still feed in aggregations (Fig. 1d) on relatively large and well developed leaves. Although many postdiapause larvae feed on shrubs bearing the previous year's webs, like other *Euphydryas* species, some disperse. Extensive, characteristic feeding damage as well as postdiapause larvae have been observed on isolated *L. involucrata* shrubs on which there had been no prediapause larvae. In the Beartooth population, some postdiapause larvae have been found feeding on *Castilleja linariaefolia* Benth. (Scrophulariaceae), *Valeriana occidentalis* Heller (Valerianaceae) and *Pedicularis bracteosa* Benth. (Scrophulariaceae). All of these plants have iridoid glycosides, secondary compounds known from the host plants of other *Euphydryas* (Bowers, 1981).

Diapause-related and postdiapause mortality appear to be quite high in Colorado. The number of postdiapause larvae found is consistently much smaller, by as much as two orders of magnitude, than the number of large third instars observed shortly before diapause. Both postdiapause larvae and pupae may be parasitized, the latter in Colorado by the hymenopteran *Ptermalus vanessae* Howard, which oviposits into mature larvae or pupae. Parasitized larvae in the Beartooth population cease feeding and movement in the fifth instar (Fig. 2c), and the *Benjaminia* parasitoid then emerges three to four weeks later.

Most, if not all, larvae in the Beartooth population return to diapause for a second winter before pupating; they spend the first winter in the second instar and the second in the fifth instar. The second diapause apparently is not obligate, but the shortness of the growing season in this habitat has led at least part of the population into a two-year life span; Williams (1981) has demonstrated another adaptation in this population for the cold climate, that of ovipositing so that the eggs are warmed maximally by the sun. A biennial life cycle has also been reported for *Euphydryas maturna* (Forster and Wohlfahrt, 1955), a close, European relative of *E. gillettii*.

Larvae generally move away from the host shrubs for pupation (Figs. 1e & 1f), and the pupation sites are usually within 50 cm of the ground. While distinctive in color and pattern, the pupae are not easily found. Pupation requires about three weeks.

Adults. The adults fly during a four week period from June to mid-August. As is typical for butterflies (Wiklund and Fagerstrom, 1977), males are the earliest to emerge and show the greatest wing wear early in the season, and the male to female ratio declines gradually through the flight season (Williams, in prep.). Males also fly earlier in the morn-

ing than females and in relatively greater numbers on cloudy days. Males are much stronger fliers; though smaller (in accord with Singer, 1982), they fly at faster speeds, are more difficult to catch, and are more difficult to manipulate when netted.

These butterflies spend much of the day sunning near the ends of branches high in coniferous trees, typically with the wings open slightly more than 180 degrees. Males fly back and forth through the habitat more than females, while females fly down to nectar more frequently. Occasional individuals puddle in the afternoon when other activity is reduced. Nights are spent in trees at heights of at least 3 m.

Mating is rarely observed because of the predilection of this species for the tops of nearby conifers. Chases of individuals near tree tops are common during the middle of the day, with males chasing both females and other males. It remains curious, though, that males infrequently chase females while females nectar in the herbaceous layer.

The butterflies do not have to move far to nectar. There is a profusion of flowers in the *E. gillettii* habitat, largely because it is moist, and they feed readily at the available blossoms. The commonest nectar source for the Wyoming populations is a white geranium, *Geranium richardsonii* Fischer and Trautvetter (Geraniaceae), which is also used in Colorado where the most important source is probably *Erigeron peregrinus* (Pursh) Greene (Compositae). After senescence of the primary nectar source, *E. gillettii* in Wyoming turns readily to yellow composites, mostly several tall *Senecio* which begin blooming as the *Geranium* cease. Given the abundance of flowers and the relatively limited time spent nectaring, adult food resources would not seem to be a major limiting factor in the population dynamics of this species.

DISCUSSION

Euphydryas gillettii was originally described and placed in the genus *Melitaea* by Barnes (1897) from material collected in Yellowstone National Park, Wyoming; *M. glacialis* (Skinner, 1921) is a synonym. Gunder (1929), in his reorganization of North American *Euphydryas*, recognized the relationship of *E. gillettii* to the other *Euphydryas* species and pointed out that it is likely the most primitive of the North American species. L. G. Higgins (1978) then revised the genus *Euphydryas* and placed *E. gillettii* in a new genus, *Hypodryas*, along with the Palearctic species *E. maturna*, *E. intermedia*, *E. eduna*, and *E. cynthia*. Phenetically, *E. gillettii* seems most closely related with those species, although comparison of early stages and allozyme frequencies would clearly be desirable.

Following good taxonomic practice we have not accepted *Hypodryas* as a genus; obligatory categories—genera, families, etc.—should be

kept conservative to facilitate communication (Ehrlich and Murphy, 1982). *Hypodryas* could be considered as synonymous with "the *matura* species group" or, at most, a subgenus. *Euphydryas* is a phenetically quite uniform group. Because the genus is now so widely discussed in the non-lepidopterological literature, we would not suggest any change in the widely accepted generic name.

Of current interest in the study of butterflies is whether or not the prior presence of eggs influences where a female lays her eggs. In several species—*Battus philenor* (Rausher, 1979), *Pieris brassicae* (Rothschild and Schoonhoven, 1977), and *Anthocharis sara* (Shapiro, 1980)—active egg load assessment is indicated, and in all of these cases females avoid ovipositing where eggs currently are or recently have been. Female *E. gillettii* rarely avoid leaves that already have eggs; moreover, the egg clusters are grouped together more than one would expect if they were distributed in the environment at random (Williams, 1981). The same is apparently true of *E. phaeton* (Stamp, 1982). Though there has been no previous support for positive egg load assessment, the grouping of eggs or egg clusters together may further enhance survivorship of larvae if there is a selective reason, such as predator avoidance or thermoregulation, for grouping the eggs together initially. Stamp (1981, 1982) has considered reasons for such a grouping, though in her experiments, *E. phaeton* suffered increased parasitism when the groupings were too large. Because the larvae from different clusters of *E. gillettii* eggs do mix freely in communal feeding webs, the contagious distribution of clusters may be adaptive.

E. gillettii displays sedentary behavior and occurs in localized colonies with few populations known; these characteristics, along with the ease with which individuals may be caught, indicate that it could easily suffer from excessive human impact. How threatened the species may be is unknown, largely because it occurs in undisturbed mountain habitat, but much reduction in numbers in any one place could lead to the extinction of local colonies. Those who find a population in the field should exercise discretion when collecting, especially with females.

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